On an abnormal cone in the Douglas Spruce, Pseudotsuga mucronata.

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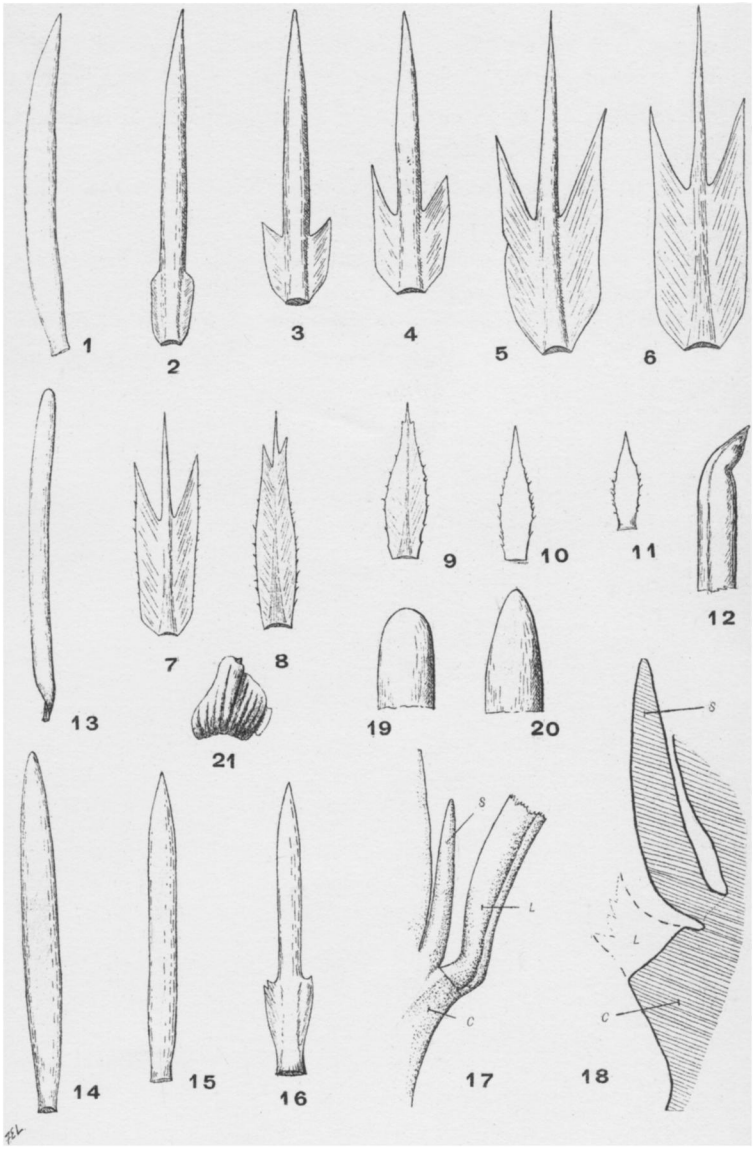
(With Plate 327.)

While studying a number of specimens of this species which had grown in a grove at Forest Grove, Oregon, the writer found a tree about 40 years old in which the leader of the year before had produced in its upper portion a cone which was abnormal both in its position and structure.

Normal cones are produced from lateral buds at the ends of twigs in the middle and lower portions of the tree. During the few days while pollination is in progress they stand upright. After pollination, however, they exhibit a downward movement till the position is entirely reversed and the cones hang down, in doing which they have assumed the position characteristic of the spruces, to which the Douglas Spruce is closely allied.

The normal cones are from 7 to 10 cm. in length and when mature and dry the scales spread to make a width of 4 to 4.5 cm. The ovuliferous scales are orbicular in outline, and are concave above. Each scale is subtended by a so-called bract, which is nothing more or less than the leaf which subtends the scale, but which differs from the ordinary foliage leaves in being expanded laterally. The character of the lateral expansion is of great interest,for we have here a structure which strongly suggests a stipular affair. So far as the topography of the bract and the ontogenetic series found in the female shoot offer evidence, it would seem that we are justified in so regarding it. At the base of the cone the lateral expansions are quite small and at the base of the bract. In ascending the cone the blade gets smaller gradually till it becomes at the top a mere point on the tip of the now triangular scale-like bracts which are quite primitive in character. That these expansions are, strictly speaking, stipules may be objected to on the ground that there is not developed therein any vascular tissue, for it has been held that the development of such tissue is a



PSEUDOTSUGA MUCRONATA.

constant feature of stipular outgrowths.* May not the leaves in conifers be regarded as exceptional, however, on account of their peculiarities in the distribution of the vascular tissue, and their manner of growth? If, however, the use of the term stipule entails the idea that the causes underlying the origin of the lateral expansion of the bracts in *Pseudotsuga* and the true stipule of the Angiosperms are the same, we have here a more serious objection and one which cannot be put away without further study. In *Abies* such an expansion of the bracts takes place, and certain features in the cones of this genus and of *Pseudotsuga* indicate that the pressure of the scales upon the bracts may account for it. This explanation is suggested by a consideration of the maturing cones of *Pseudotsuga*. During the growth of the cone after fertilization, the pressure of the scales upon the bracts, which continue to grow at their bases, increases and they become narrower and more constricted wherever this increased pressure is brought to bear upon them. This is, of course, in their lower parts which are not exserted.

As to the function of these bracts it may be said that, while they are undoubtedly assimilative to some degree both before and after anthesis, they serve more especially as guides to lead the pollen to the micropyles during pollination. In this regard, therefore, they are far different from the stipules of angiosperms.

The transverse section of the upper or laminar portion of a bract shows that the bracts conform to the leaves in their plan of structure, but do not develop any supporting cells in the interior. This is correlated with the fact that the bracts do not support themselves in the more or less horizontal position in which the ordinary leaves are placed, but simply hang down. The parenchyma, moreover, consists of spherical cells and there is no well defined palisade tissue nor stellate cells.

A similar section taken through the stipular region shows the same features, and shows in addition the character of the lateral expansion, which consists of a thin extension of the spherical parenchyma cells bounded above and below by the epidermis. The endoderm is here but poorly developed, while in the lamina

* "The Nature and Origin of Stipules," A. A. Tyler, Ann. N. Y. Acad. Sci., 10: 1–49. 1897.

the sheath is continuous and fairly well formed. The foliage leaves, on the other hand, have a strongly developed hypoderm which is absent only in the regions in which are found the stomata.

The abnormal cone, which, as has been stated, was produced in the upper portion of the leader, is 45 mm. long, and is made up of seminiferous scales subtended by slightly modified leaves. The scales in the lower portion of the cone are somewhat irregular but differ only in a minor degree from those in the normal cone, while as we pass upwards they become smaller and somewhat irregular and scattered. That they become scattered is due to the failure of the scales to develop in some cases, although a close examination of the axils of the leaves in these cases will discover small structures of bud-like appearance. That these structures are the morphological equivalents of buds, their origin and position strongly attest. That they would, upon further development, have become ovuliferous scales is equally sure.

There can be no doubt, therefore, that the scales are developed from the axils and not from the upper faces of the leaves. The scale is, therefore, not "an appendage, a ventral excrescence, a ligule if it may be so called, of a leaf,"* but rather a reduced and modified branch. In support of the view, first advanced by A. Braun, that the scale represents two connate leaves, it may be said that the irregularity of the scales, when such irregularity occurs, seems to be due in each case to unequal growth of the two halves. This is what would be likely to happen under a slight irregularity of nutrition. Furthermore, the line of connation can be traced in one case by a ridge along the inside of the scale.

In several of the scales ovules were produced, but these failed of fertilization, and so no seeds were matured.

The scales are subtended by leaves which differ from the normal leaves in having acute apices and in some cases in being slightly expanded in the lateral portions. In the production of these characters, however, a strong attempt has been made to copy in every respect the normal cone in which the leaves are modified in just this way but to a greater degree. The amount of lateral expansion undegone by the various cone-leaves is greatest

* Eichler: Monatsber. d. k. Acad. d. Wiss. Berlin, 1881.

in the thickest part of the cone, paralleling in this regard the case of the normal cone.

Below the base of the cone for the distance of 1 cm. are found foliage leaves with acute apices (Fig. 15). Further still below, the leaves approach more closely to the normal shape (Fig. 14), but still differ in having somewhat acute apices (Fig. 20).

The leader involved is bent so as to suggest that some accident overtook it during its growth. The bracts are quite sharply bent at their tips (Fig. 12), as if they too had shared the leader's misfortune. At the top of the leader were produced normal terminal and lateral buds which developed in the usual way the following spring.

We have, then, in the structure upon which the above description is based the result of the sudden assumption of the sporophyllary function by the tissue of a normally strictly negative shoot. We have here to do with the question which has grown out of Bower's* view that foliage leaves are secondary structures produced by the sterilization of the sphorophylls.

Bower has been followed by Atkinson,† who has attacked the problem from the point of view of the experimental morphologist, and has discussed the relation of the sporophyte to nutrition. Professor Atkinson's convictions in the matter are based to a considerable extent upon experimental work upon two species of *Onoclea*, in which the sporogenous leaves were made to take on the assimilative condition by cutting away the earlier and normally assimilative leaves and thus robbing the plants of food which they would otherwise get. The condition thus induced is compared directly with the probable conditions under which the sporophyte was made to assume more and more the assimilative function when the change from water to dry land was one with which the gametophyte was unable to cope.

The conversion of a vegetative shoot in a conifer to a sporophyll-bearing shoot is of peculiar interest in this connection in that it must have some bearing upon the view propounded by Bower. In the coniferae only a few lateral buds are normally produced

*Bower: "A Theory of the Strobilus in Archegoniate Plants." Ann. Bot., 8 343. 1894.

†Atkinson: Woods Holl Biol. Lect. 1895. Am. Nat. 30: My. 1896.

near the ends of the vegetative shoots. In the pistillate shoots, however, the axillary buds, throughout the greater part of its length, are developed into the ovuliferous scales. The production of these scales, therefore, upon a shoot normally vegetative would seem to be due to excess of nutrition, in response to some sort of irritation. Why the axillary buds thus forced into growth should not become simply vegetative, instead of spore-bearing, may be due to inherited tendencies, and if so, we have here a case of atavism, a return to a condition during times long gone by, when the sporophyte was chiefly or altogether sporogenous. Unfortunately for this view, there is no little difficulty to be encountered in harmonizing the facts derived from the study of teratological conditions found in the angiosperms, as, for example, the change from carpel to foliage leaf. All that we can assert at present is the interchangeable character of plant structures.

Explanation of Plate 327.

FIGS. 1–11 inclusive. A series of bracts from the pistillate shoot.

FIG. 1. Leaf from pistillate shoot immediately below the cone.

FIG. 2. Bract from base of cone.

FIG. 11. Bract from tip of cone.

FIG. 12. Lateral view of the apex of a bract from the abnormal cone.

FIG. 13. Normal leaf, × 3/2.

FIG. 14. Leaf from the leader which produced the abnormal cone.

FIG. 15. Leaf taken from the leader immediately below the abnormal cone.

FIG. 16. Leaf subtending a scale in the abnormal cone showing the maximum degree of lateral expansion attained.

FIG. 17. A small portion of the leader bearing a leaf and, in its axil, a reduced scale, × 15/1, *s*, scale; *l*, leaf; *c*, leaf-cushion.

FIG. 18. Longitudinal section of same, × 20/1 about. Drawn with camera lucida.

FIG. 19. Tip of normal leaf, × 6/1.

FIG. 20. Tip of leaf from leader in question, × 6/1.

FIG. 21. An abnormal, asymmetrically developed scale showing discrepancy of growth between the two sides, × 3/2.